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Ecology and the Atomic Age

Actually, the atomic age can well provide the means of solving the very problems it creates.

—EUGENE P. ODUM, "Ecology and the Atomic Age"

Atomic energy today is still largely military; unfortunately, it has proved to make much better weapons than plowshares.

—EUGENE P. ODUM, "Radiation Ecology at Oak Ridge"

"THE AGE OF ECOLOGY began on the desert outside Alamogordo, New Mexico, on July 16, 1945, with a dazzling fireball of light and a swelling mushroom cloud of radioactive gases."[1] There is an element of truth in this provocative claim made by Donald Worster in the epilogue of his fine book, *Nature's Economy*. The potential dangers to health and environment posed by atomic energy were quickly recognized and eventually served as a primary target of popular environmental movements. In response, professional ecologists effectively used concerns over atomic energy as a convincing justification for ecosystem studies. But the "Age of Ecology" and the "Atomic Age" coincide for important reasons other than that suggested by Worster. Atomic energy also provided ecologists with an exciting new set of tools, techniques, and research opportunities. Thus, for the professional ecologist of the postwar period, nuclear power appeared to be a kind of double-edged sword: capable of wreaking environmental havoc, but also capable of unlocking many of nature's secrets for human benefit.[2] Perhaps even more important than these technical innovations were the economic opportunities of the atomic age. In the decades after World War II, the Atomic Energy Commission (AEC) became an important source of funding for ecological research. Ecosystem ecology clearly benefited from its association with one of postwar Washington's high-profile agencies, but the relationship was by no means asymmetrical. As Eugene Odum suggested in 1965, during the decades following World War II a feedback loop developed between nuclear power and ecology.[3] One might also think of a form of symbiosis developing between atomic energy and ecosystem ecology—a relationship in which both partners benefited. This chapter traces the development of that relationship.

The Metabolism of Ecosystems

As the United States entered World War II, Raymond Lindeman presented ecologists with a promissory note. His measurements of productivity and trophic efficiency were only rough estimates, but he had shown that such measurements could be made. By doing so the ecologist could discover something important about how ecosystems function. This promissory note was cashed a decade later by two brothers on a tiny speck of land a quarter of the way around the globe from New Haven. Eugene Odum and Howard Odum (figure 9) were not the only ecologists interested in studying energy flow in ecosystems after World War II; however, their study of a coral reef on Eniwetok Atoll appeared first, and it won the prestigious Mercer Award from the Ecological Society of America. Thus, it became an important exemplar for the new type of functional study of ecosystems that became so popular during the 1950s.

Eniwetok Atoll is a collection of some thirty tiny islands protruding from a horseshoe-shaped coral reef surrounding a shallow lagoon.[4] A distance of roughly twenty-five miles separates a wide, shallow inlet at the southern end of the horseshoe from the northernmost island at the top. During World War II, Eniwetok was an important military base, first for the Japanese and later for the United States. After the war, it became a site for testing nuclear weapons.[5] The largest island in the atoll, Eniwetok, served as a base for air support during the earliest postwar tests carried out during the summer of 1946 on Bikini Atoll, two hundred miles to the east. Later Eniwetok Atoll itself became a major testing site. Operation Sandstone, a series of tests begun in 1948 on a new generation of more efficient fission bombs, was carried out on islands in the northeast quadrant of the atoll. And in 1952, as part of Operation Greenhouse, the first thermonuclear device was detonated on the atoll. The 10.4 megaton blast obliterated the island of Elugelab, vaporized millions of gallons of ocean water in a fireball three miles in diameter, and gouged a crater half a mile deep and two miles long in the reef.[6] Atmospheric testing of nuclear weapons in the Marshall Islands continued throughout the decade and culminated in a series of thirty-three explosions during the summer of 1958.[7]

With the advent of nuclear testing, the Marshall Islands became a center for extensive biological, geological, and oceanographic research. Concerned with the potential effects of radiation on biological systems, a task force of scientists drawn from universities, private research institutes, and government agencies completed an initial survey of Bikini and neighboring atolls in 1946.[8] Subsequent studies were carried out during the period of atmospheric testing. As part of this research effort, the Atomic Energy Commission approached Eugene Odum to undertake a detailed ecological study of Eniwetok.[9] Odum, a professor of zoology at the University of Georgia, was already under contract with the AEC to do ecological research at the Savannah River nuclear reservation. Together with his younger brother Howard, an ecologist at the University of Florida, Odum spent six weeks in 1954 studying a reef on the windward side of the atoll. By time they arrived on Eniwetok, the atoll was hardly a pristine natural environment. Indeed, it was sufficiently radioactive that the Odums produced an autoradiographic image of a coral head simply by placing it on photographic paper. In a bit of understatement, the two ecologists introduced their report with the statement that the ongoing nuclear testing at Eniwetok provided a unique opportunity "for critical assays of the effects of radiations due to fission products *on whole populations and entire ecological systems in the field*."[10]

Although neophytes in radiation biology and almost totally unfamiliar with the ecology of tropical reefs, the Odum brothers were better prepared than most ecologists for the type of project proposed by the AEC. Both were already working on major ecosystem studies in the United States. Beginning in 1951 Eugene had initiated what became a long-term study of succession and productivity on farmland abandoned during the construction of the Savannah River nuclear facility. Howard was in the midst of an even more ambitious study of warm mineral springs in Florida.[11] Although his four-year study of Silver Springs was published two years after the Eniwetok study, by 1954 he had already perfected a number of techniques that the brothers used to study the metabolism of the coral reef. A student of G. Evelyn Hutchinson, Howard Odum shared his teacher's penchant for making bold theoretical speculations and then testing their consequences with equally bold experimental studies. Eniwetok provided Howard with a perfect opportunity for exploring not only Lindeman's theoretical claims but also some of his own controversial ideas about the nature of ecosystems. It is also significant that the Eniwetok study came a year after the publication of Eugene's *Fundamentals of Ecology* (1953). The chapter on energy, written by Howard, outlined general principles and provided a few examples. These examples, however, were constructed from miscellaneous data collected from several unrelated sources. Prior to 1954, no one had investigated a complete ecosystem with the intent to measure its overall metabolism. Eniwetok and the Atomic Energy Commission provided the opportunity to do so.

The Odums have often claimed that ecosystem ecology is predicated upon an antireductionistic, "whole-before-the-parts" philosophy,[12] but the Eniwetok study actually demonstrated how readily the Odums moved among levels of organization. In reality, the parts and the whole were equally important, and both were investigated simultaneously. The study was holistic in the sense that its primary focus was the overall structure and function of the ecosystem. The metabolism of the entire reef was most important, not the metabolism of constituent individuals or populations. In fact, the Odums were so unfamiliar with corals that they could not identify most species on the reef.[13] In a very real sense, the reef at Eniwetok Atoll was a "black box" whose total inputs and outputs of energy were being measured.[14] But understanding the whole could not be accomplished without understanding at least some of the parts. The Odums may not have known the scientific names of the corals, but they were interested in the functional role played by this important component of the ecosystem. Indeed, the peculiar nature of coral held the key to understanding the system as a whole.

In antiquity corals were considered plants, but zoologists, recognizing them to be coelentorates, had long claimed them for their own. Early in the twentieth century it was discovered that coral polyps often contained symbiotic unicellular algae. Functionally, if not taxonomically, the polyp had to be considered "part plant."[15] For the Odums this was not merely a curiosity; it suggested a pervasive symbiosis. Existing in the inert calcium carbonate skeleton surrounding the coral polyps were networks of filamentous green and blue-green algae. These were sufficiently dense that the entire coral head often had a distinctly greenish hue. Previous investigators had dismissed the filamentous algae as parasites that actually weakened the coraline skeleton. But the Odums suggested an alternative explanation: mutualism. Although they could not actually demonstrate a transfer of nutrients, the ecologists proposed that the algae shared the products of photosynthesis with the coral polyps. In exchange, the polyps protected the delicate filamentous algae from browsing predators, intense sunlight, and other environmental hazards. Some indirect evidence supported this claim. Autoradiographs demonstrated that the radioactivity from the water was restricted almost entirely to the polyp zone, barely penetrating to the algae beneath the polyp. Where living polyps were absent in the coral head, however, the embedded algae were intensely radioactive.

The coral head could be considered a kind of ecosystem within an ecosystem. The amount of plankton in the water flowing over the reef provided insufficient food to support the coral animals. Thus, the metabolic economy of the head depended upon the photosynthetic production of symbiotic algae. The complex structure of the head provided a mechanism for recycling basic nutrients to these producers; the small leakage of nutrients escaping from the system was just balanced by nutrients entering the reef from the ocean. An earlier survey of Eniwetok Atoll had suggested that the entire reef might also be self-supporting. Compared to the reef, the open ocean was not very productive; it probably was not a major supplier of organic material for the coral. This finding was, however, inconclusive. Put simply, there were two possibilities. Perhaps the reef was a highly efficient filtering mechanism, and even though there was little organic material in the ocean water, the large volume of water passing over the reef might yield a significant food supply for coral polyps. In economic terms, this scenario suggested that the ecosystem was operating at a deficit, sustained by energy and nutrients imported via the oceanic current. Alternatively, the community might be truly self-sufficient, recycling necessary nutrients within itself and living off the photosynthetic production of its algae. Choosing between the alternative explanations required the construction of an energy budget for the reef, as a whole. If productivity did not at least equal respiration, then the community was not self-sustaining.

Water samples from the front and back of the reef contained almost the same amount of nutrients. This suggested that the coral was not simply filtering food imported from another ecosystem. More important, using an ingenious technique perfected by the younger

Odum, the two ecologists demonstrated that the productivity and respiration of the reef were nearly equal. Howard Odum's "diurnal flow" method rested upon the notion that the reef was like a river; water flowed from "upstream," at the front of the reef, to "downstream," at the back of the reef.[16] Simultaneous determinations of dissolved oxygen in front of the reef and behind could be used to measure the overall metabolism. An increase in oxygen indicated that rate of photosynthesis was greater than the rate of respiration. A decrease indicated that respiration was occurring at a more rapid rate than photosynthesis. Periodic measurements of dissolved gases taken during a twenty-four hour period could be combined to form an energy balance sheet for the living community. Oxygen determinations taken at night, when no photosynthesis occurred, provided a measurement of the rate of community respiration. Those taken during the day, when both processes occurred, provided a measurement of net primary production. Adding community respiration (determined at night) and net primary production (determined during the day) gave the total or gross primary production for the ecosystem. Using these determinations, the complete energy budget for the reef could be estimated. Expressed in terms of grams of glucose/meter^2/day, the Odums's calculations indicated that the energy income of the reef was slightly higher than its losses. Although the energy budget was slightly out of balance, indicating that the community actually produced slightly more than it consumed, the Odums admitted that the methods used were not sufficiently refined to support this conclusion with any degree of confidence. Indeed, they favored the view that the reef was a true steady state ecosystem or in more traditional ecological terms a climax community.[17] This did not mean that the reef was a static system—far from it. The visible biomass, or standing crop, represented only a small fraction of the energy captured by producers. The Odums estimated that there was a complete turnover of biomass more than once a month on the reef. As the Harvard ecologist George Clarke had earlier suggested, the ecosystem might be likened to a factory filled with spinning wheels.[18] But it was a rather strange factory, for virtually all the ecosystem's production was used to maintain the machinery. Little was stored as visible biomass.

The Eniwetok study was a landmark in ecological research, important to both individual researchers and the discipline of ecology as a whole. The reef with its close symbiotic relationships between coral and algae was an excellent example of a highly structured, self-regulating system—a nascent view of ecosystems toward which both

Odums were strongly attracted. Over millions of years, the Odums reasoned, the reef had evolved an optimum composition of interacting species, a composition that favored the stability of the whole. According to this "stability principle," natural selection amounted to "survival of the stable."[19] By favoring stability, natural selection perfected self-regulating interactions in ecosystems. This belief in ecosystem stability, a belief shared with G. Evelyn Hutchinson and several other ecologists, is discussed in greater detail in chapter 7. Suffice it to say that the experience at Eniwetok focused and reinforced ideas that the Odums already held about the fundamental nature of ecosystems. For Eugene, the coral reef became an exemplar for self-regulating, self-maintaining systems.[20]

If Eniwetok was an important milestone in the careers of Eugene Odum and Howard Odum, then it was equally significant as an indicator of where post–World War II ecology was heading. The Mercer Award has often gone to ecologists whose research establishes new trends. The Odums's paper, which won the award in 1956, was the first of several similar studies. It was followed two years later by Howard's monumental study of Silver Springs, certainly the most ambitious ecosystem study of the 1950s. Supported by a $20,000 grant from the Office of Naval Research (ONR)—a substantial sum for that time—the younger Odum had spent four years studying the flow of energy and materials in this aquatic system. During the course of this work, Howard not only developed the techniques used at Eniwetok, but he also produced the most detailed account of the energy flow and nutrient cycling in an ecosystem. It remains the ecosystem study most commonly referred to in undergraduate textbooks. Other studies during the 1950s by ecologists such as John Teal, Frank Golley, Lawrence Slobodkin, and Edward Kuenzler also helped to establish energy flow as a central area of research within the discipline.

The case of John Teal is particularly significant for what it reveals about the emergence of a self-conscious group of ecosystem ecologists. Teal, a graduate student at Harvard University, had begun physiological research using leeches. As he later recalled, he quickly became bored with his rather traditional laboratory project. After reading Lindeman's trophic-dynamic paper, probably in 1952, Teal became excited about studying the "metabolism" of a more complex biological system: a small cold spring near Concord, Massachusetts.[21] Like the Odums, who were beginning their research projects at the same time, Teal wanted to make a more precise functional analysis of an ecosystem than Lindeman had been able to do. Such detailed studies of energy flow, Teal hoped, would allow ecologists to understand ecosystems in the same way that traditional metabolic studies allowed laboratory physiologists to understand how individual organisms functioned.[22] The system that Teal chose to study was ideal for the purpose. Only two meters in diameter, the spring was as close as nature could come to being a "laboratory ecosystem."[23]

During his two-year study, Teal was unaware that several other ecologists were doing much the same type of research. Although he had been introduced to Lindeman's paper by his adviser, George Clarke, he did not discuss it with either Clarke or other ecologists. Only after completing the field work did he meet Howard Odum, whose influence can be seen in the diagrammatic presentation of Teal's data. By 1957, when Teal's study and Odum's Silver Springs paper appeared in *Ecological Monographs*, an informal network of ecosystem researchers was beginning to form. On Howard's recommendation, Teal was hired as a postdoctoral fellow by Eugene Odum, who was building a marine laboratory on the Georgia coast. Together with several other young Ph.D.s and graduate students Teal established the laboratory on Sapelo Island and began one of the first ecosystem studies of fragile and environmentally important salt marshes.

New Economic Opportunities

The Eniwetok study served as an early benchmark for ecosystem studies, but for the historian it also serves as a symbol for post–World War II science. Academic science in America was revolutionized by the war. Scientists had been mobilized on a large scale, and they had contributed decisively to winning the war. For scientific planners facing the uncertainties of the post–war world, military strength, economic growth, and human welfare seemed to depend upon this new partnership between the state and the scientific community.[24] For individual scientists, including ecologists, the postwar period was also a watershed. If, as Robert McIntosh suggests, the classical ecologist was a rugged individualist working with a few pieces of string and a pH meter,[25] the image of the new ecologist was quite different. Not only did "fancy instruments with flashing lights and clicking sounds" become part of the ecologist's tool kit,[26] but in the new environment of government contracts and grants, the successful scientist had to combine the skills of investigator, entrepreneur, and bureaucrat.

For ecosystem ecologists this new environment offered many opportunities for building research programs. During the period from

1950 to 1965, the "golden age" of funding, several government agencies vied for the opportunity to support innovative basic research in biology.[27] Even in agencies such as the Office of Naval Research, which funded Howard Odum's Silver Springs study, there was strong commitment to supporting innovative research regardless of its direct military application. Recalling his role in setting research priorities at ONR, the oceanographer Roger Revelle noted:

> Helping the Navy was not a good reason for doing research. The only good reason for doing research was that they [scientists] wanted to do it in their bellies; they were driven by curiosity, the desire for discovery and the desire for fame, which is what drives scientists. . . . In fact, we had two or three different mottos in my part of the ONR. One was that any proposal for less than $5,000 we automatically funded. Another was, as I say, that anybody who said he wanted to do this because it was good for the navy we automatically turned him down, unless it was for less than $5,000.[28]

Revelle's recollections, forty years after the fact, may be slightly romanticized. But throughout the 1950s there was a sense of excitement in many funding agencies; there seemed to be unlimited opportunities for supporting basic science, and great things seemed possible as a result of this new partnership between science and government.

No federal agency epitomized this attitude as well as the Atomic Energy Commission. Beginning in 1948, two years after the agency was established, its Division of Biology and Medicine began supporting a diverse program of research in the life sciences.[29] Support for ecology never rivaled that for genetics or physiology, but impressive research programs were started at a few universities and national laboratories located at Oak Ridge, Brookhaven, Savannah River, and Hanford. Much of this research was directed toward applied problems of radiation ecology, an area of research that had gained limited support even during the war.[30] However, as the case of Eugene Odum at the University of Georgia illustrates, ecologists interested in basic science could also benefit from the largesse of the Atomic Energy Commission. Combining the opportunities provided by the Savannah River nuclear facility with other unique local sources of funding, Odum created one of the most influential programs in ecology. This was done within the structure of a small state university, an institution that otherwise would have provided a poor environment for building such a program.

The Savannah River nuclear facility was built as a result of President Truman's decision in 1950 to begin production of the hydrogen bomb.[31] The primary function of the plant was to produce tritium for the new bomb, but plutonium was also to be produced there. Construction began on the site in Aiken, South Carolina, in the spring of 1951, and the first of five reactors began operating two years later. Because the Savannah River facility was an entirely new facility, it provided a unique opportunity for doing pre-installation environmental surveys; that opportunity had not been considered during the wartime push to build the first atomic weapons.[32] Early in 1951, the AEC invited proposals for ecological research from the Universities of Georgia and South Carolina.

Eugene Odum submitted a detailed proposal for an ambitious environmental survey of the terrestrial and aquatic ecosystems surrounding the Savannah River facility. The initial survey would be followed by subsequent studies once the nuclear reactors were operational. Thus, Savannah River would serve as a kind of large-scale experiment to determine the effects of emitting low levels of radiation and large amounts of heated water into the environment. Odum's proposal called for six full-time principal investigators supported by graduate research assistants. The initial annual budget for the project, to be shared by the AEC and the university, was estimated at slightly more than $267,000.[33]

Two decades later a grant proposal of this magnitude would not have raised eyebrows, but in 1951 the AEC was not contemplating an environmental impact statement. Odum's proposal was rejected, and in a subsequent meeting with AEC officials he was informed that the commission was prepared to provide a yearly grant of approximately $10,000 to prepare an inventory of the animal populations in the area. A similar amount would be given to the University of South Carolina for botanical work. Odum was able to convince the commission to use some of the money to support a study of secondary succession on the abandoned farm land surrounding the plant. He also expressed interest in experimenting with radioactive tracers, a technique he knew little about but one that he and his students later used extensively.

As Odum recalled, enthusiasm for the project quickly declined on campus when it was learned that the university would not receive a $150,000 "sugar plum" from the government.[34] Apparently this was also the case at the University of South Carolina, which dropped out of the project after only a few years. Odum, however, pushed ahead and submitted a much more modest proposal to the AEC. He also made a strategic decision that, in retrospect, insured the success of his research program. The limited money provided by the AEC would not be used to support senior researchers; faculty members would continue to be paid by the university. Instead, virtually the entire research budget was earmarked for graduate assistantships. As a result, Odum was able to attract a steady stream of students to his fledgling ecology program.

What began as a small and uncertain source of support, rapidly developed into a long-term relationship between the University of Georgia and the AEC. By 1960 the annual budget for ecological research at Savannah River had increased to $60,000, and the AEC had agreed to establish a permanent ecological laboratory at the site. Frank Golley, a young faculty member at the university, became the resident director of the laboratory. Golley, a recent graduate of Michigan State University, had studied energy flow through a single food chain in an old field community. His dissertation was perhaps the first attempt to study the metabolism of a terrestrial community. Odum, who had met Golley on a visit to Michigan State, was instrumental in bringing the young ecologist to the University of Georgia. The two shared not only an interest in the developing specialty of radiation ecology but also a broader commitment to ecosystem ecology. Golley was, therefore, the perfect choice to direct the expansion of the ecological research program at Savannah River.

One can only speculate about how successful Eugene Odum's research program would have been without the long-term support of the AEC. It seems safe to say that the University of Georgia would not have become such a major center of ecological research were it not for atomic energy. But the Atomic Energy Commission was only part of the equation for success. In contrast to the Oak Ridge and Hanford laboratories, ecological research at the University of Georgia never became narrowly identified with radiation ecology. To a large extent, this was owing to the fact that Odum, Golley, and other ecologists at the university had a much deeper commitment to ecosystem studies than to radiation ecology per se. Contract work at Savannah River was viewed, not as an end in itself, but as a means to help subsidize the broader ecological program at the university.[35] The subsidy was more than just economic. The laboratory at Savannah River provided research opportunities for graduate students and served as a kind of training base for young Ph.D.s. Those who made good were often brought back as faculty members on campus. Geography helped too; being separated from the university campus by more than one hundred miles, the Savannah River operation could be maintained as a semi-autonomous part of the larger research program. Finally, although funding from the Atomic Energy Commission was crucial, it was not the only source of support for the ecology program that Odum was struggling to build during the 1950s.

Eugene Odum had a knack for taking advantage of regional opportunities. Trained as an ornithologist, Odum and his students used Sapelo Island, a marshy piece of land on the Georgia coast, as a study area. The island was owned by R. J. Reynolds, Jr., who used it as a hunting preserve. During the course of his visits to the island Odum got to know the tobacco heir, and in 1954 Reynolds donated Sapelo to the state of Georgia and established the Sapelo Foundation to support ecological research on the island. Like Savannah River, research on Sapelo Island began modestly. John Teal, one of the first ecologists to arrive, found that the "laboratory" was an old barn with a scale, microscope, and few other pieces of equipment.[36] The laboratory did provide access to a nearly pristine salt marsh, however, and the island continued to draw graduate students and young Ph.D.s eager to do ecosystem research in this unique natural environment. The Sapelo Foundation might not have provided the level of funding that the AEC did, but Odum used the money in the same way to expand graduate and postdoctoral research at the University of Georgia.

Looking back on the origins of his program, Odum noted the irony of a major center of ecological research based at a small university in Georgia.[37] To a certain extent, his success as a scientific entrepreneur was fortuitous. Savannah River and Sapelo Island provided Odum with unusual opportunities unavailable to most other ecologists. But Odum skillfully built upon this foundation. By the early 1970s his Institute of Ecology was attracting several million dollars in support from a wide variety of federal, state, and private agencies.

During the early 1950s Odum was unique among ecologists in the level of support that he received from the AEC. This situation began to change around the middle of the decade. In 1955 John N. Wolfe, an ecologist at Ohio State University, became an administrator in the Division of Biology and Medicine.[38] Three years later he was promoted to chief of the newly established Environmental Sciences Division at the AEC. Under Wolfe's energetic leadership the scope of AEC, funding in ecology greatly expanded, particularly support for university-based research. Just as significantly, during this period ecological programs at the national laboratories expanded, particularly at Oak Ridge.

As Chunglin Kwa has shown, despite its similarities to the University of Georgia program, the development of the Oak Ridge ecology program was constrained by its unique setting.[39] In 1954, Stanley Auerbach was brought to Oak Ridge to develop research on the movement of radionuclides in the environment. Auerbach's position was more tenuous than Eugene Odum's. The Oak Ridge National Laboratory (ORNL) was strongly oriented toward the physical sciences, and it was headed by the egocentric Alvin Weinberg. Weinberg had little interest in biology, although he believed that environmental studies might play a small, but significant, part in his scheme for making the laboratory a center for "big science." Despite these institutional constraints, Auerbach skillfully built an impressive ecological program. Ecologists at Oak Ridge often held joint appointments in biology departments at the University of Tennessee. This provided access to students and gave the program an academic dimension. Auerbach also used his position as secretary of Ecological Society of America to raise the visibility of the program in professional circles. Intellectually Auerbach drew heavily upon the ideas of Eugene Odum, who served as a consultant to the Oak Ridge program, but in important ways the two programs were different, a reflection of the influence of the physical sciences at the Tennessee laboratory. By the late 1960s Oak Ridge was a leading center for the study of radiation ecology, and its ecologists were pioneering the use of computer simulation, which eventually became the subspecialty of systems ecology. During the early 1970s the Oak Ridge group played a central role in organizing the large-scale ecosystem studies associated with the International Biological Program (IBP). These later developments are discussed more fully in chapter 9.

New Tools for the Ecologist

The Atomic Energy Commission provided crucial financial resources for the institutional development of ecosystem ecology. But the atomic age also provided ecologists with an array of exotic new techniques for their research.[40] Some had relatively limited applications. Eugene Odum and others experimented with the use of radioactive "tags" for tracking the movements of animals and estimating population densities. As director of the new Geochronometric Laboratory at Yale University during the early 1950s, Edward Deevey began using radiocarbon dating in his analysis of pollen in sediments of Linsley Pond. This provided Deevey with a more precise technique for attacking the paleoecological problems that he had begun to study in the late 1930s.

Radiation could also be used to study the effects of stress on living systems. Given public concerns about fallout, radioactive waste storage, and nuclear war, it is not surprising that radiation effects became one important focus of ecological research during the 1950s and 1960s. Not only were the radiosensitivities of individual organisms studied but also those of whole ecosystems. In a number of cases, natural areas were irradiated to determine damage and recovery of constituent species after exposure to radiation.[41] For example, two sites at the Brookhaven National Laboratory were exposed to high levels of radiation for a period of six months. In both cases, a forested area and an old field, a source of gamma rays (^{137}Ce or ^{60}Co) was stored in an underground lead-shielded container. The radiation source could then be raised or lowered by remote control. The Brookhaven study and similar experiments in Georgia and Puerto Rico demonstrated that at least some species of plants were relatively sensitive to radiation damage. It also suggested that succession, food chain dynamics, and diversity might be adversely affected by chronic exposure to even fairly low levels of radiation.[42]

For most ecologists involved with atomic energy, however, the most exciting application of radiation was in tracer studies. For ecosystem ecologists radioactive tracers appeared to be a powerful tool, one that held great promise for unraveling the complex internal processes of the ecosystem. "Radioactive tracers have already been well exploited by the physiologist," noted Eugene Odum in 1959, "but the ecologist is just beginning to develop techniques for studies in 'community metabolism.'"[43]

Radioactive tracers revolutionized many areas of biological research after World War II.[44] Even before the war, radioactive isotopes had been widely used as tracers to study the metabolism of plants and animals. Because radioactive isotopes are readily detectable and have the same chemical properties as their nonradioactive analogues, the use of tracers transformed the study of metabolic pathways. During the 1930s this new physiological methodology was widely discussed in general scientific periodicals such as *Nature* and *Science*, and it is perhaps not surprising that ecologists such as G. Evelyn Hutchinson, who were interested in the "metabolism" of ecosystems, soon began experimenting with radiotracers. But prior to World War II, the availability of isotopes was limited. In 1941, Hutchinson's initial attempt to study the phosphorus cycle in Linsley Pond using a radioactive tracer (^{32}P) failed when the cyclotron at Yale produced only half the amount of isotope required for the experiment.[45] After World War II the situation changed dramatically. Nuclear reactors provided an almost unlimited supply of radioactive isotopes for biological research. The distribution of these isotopes for research became the centerpiece of the government's Atoms for Peace program, and AEC officials actively promoted the use of this new technology.[46] For ecologists, the buffer zones around nuclear facilities provided large natural areas where radioactive tracers could be used for ecosystem experimentation. University researchers such as Hutchinson and his students successfully exploited the use of tracers. But given the close proximity to sources of radionuclides and the availability of large, isolated areas for field research, it is not surprising that the ecologists at the nuclear reservations at Oak Ridge, Hanford, Brookhaven, and Savannah River were at the forefront of the postwar development of ecosystem tracer studies.

Radioactive tracers provided ecologists with a means for quantifying the movement of materials and energy through the ecosystem. This new technique was particularly useful for studying biogeochemical cycles in aquatic ecosystems. The radioactive isotope of an essential element such as phosphorus could be added directly to the water. The movement of the isotope through the various trophic levels of the community, and between the community and the abiotic environment, could then be monitored with a radiation detector.[47] This added a new dimension to biogeochemical studies, for it provided the ecologist with a much clearer picture of the dynamics of the cycle. By following the movement of the tracer from one compartment of the ecosystem to another, the ecologist could more accurately estimate the rates at which these movements occurred.

While tracers could be used to measure directly the movement of materials through the ecosystem, they could also be used to measure indirectly the flow of energy. Plants, the producers in the ecosystem, were labeled with a radioactive isotope. At subsequent time intervals the various consumers in the community were then sampled for radiation. This type of study yielded two important types of information about the internal workings of the ecosystem. First, it could be used to isolate individual food chains. If a particular species of plant was labeled, then only herbivores feeding on the plant and the carnivores feeding upon those herbivores would later become radioactive. Second, tracer studies could be used to answer the question: How long does it take for energy to move through the ecosystem? By continuously monitoring the various animal populations for radiation, one could estimate the time required for elements originally in the plants to reach the end of a food chain. In short, ecologists used tracers in much the same way that biochemists and physiologists did, but on a much larger scale. By following the movement of tracer elements, the ecologist could accurately determine the actual pathways of energy flow, the rates at which the energy flowed, the amount of time that various elements remained within particular compartments of the ecosystem (residence time), and rates at which these elements moved from one compartment to another (turnover rate).

Figure 1.
Henry Chandler Cowles, 1913 (negative no. DN 60,959, Chicago Historical Society).

Figure 10.
Gene Likens (*left*) and F. Herbert Bormann (*right*) at Hubbard Brook (F. Herbert Bormann).

Tracer studies worked best in small, isolated ecosystems populated by relatively sedentary organisms. G. Evelyn Hutchinson's favorite study site, Linsley Pond, was a perfect place for such research. After the war, when a reliable supply of radioactive phosphorus could be procured from the Oak Ridge nuclear facility, he and his graduate student Vaughan Bowen were among the first to publish isotopic studies of phosphorus cycling. Even more ideal systems could be created in the laboratory. Some of the neatest data on the movement of phosphorus came from Robert Whittaker's aquarium studies at the Hanford laboratory.[48] In these microcosms, the radioactive isotope could not escape, and the fate of all the phosphorus added to the system could be accurately determined. But other ecologists were not deterred by the technical problems posed by complex natural ecosystems. The popularity of tracer studies is evident by the large number of papers on biogeochemical cycles and energy flow presented at national symposia on radiation ecology.[49]

Justifying Ecosystem Research

If atomic energy provided new research opportunities for ecosystem ecologists, then it also provided a convincing justification for their new specialty. Despite government efforts to promote "Atoms for Peace" during the 1950s, most Americans continued to associate atomic energy with bombs.[50] Latent fears about the effects of fallout and waste disposal fueled an undercurrent of uncertainty that occasionally flared into public controversy. Although ecologists could offer no panaceas, they could hold out the promise that further research might provide solutions to the environmental problems posed by atomic energy. At the forefront of this movement was Eugene Odum who did much to publicize the environmental effects of radiation in his popular textbook, *Fundamentals of Ecology*.

Fundamentals of Ecology changed in some significant ways as it went through three editions between 1953 and 1971. The most striking change in the second edition was the addition of an entire chapter on radiation ecology. By 1959 when the new edition appeared Odum had developed strong ties with the AEC, but there was nothing in his rather traditional academic training that had prepared him to be a radiation ecologist. His introduction to the subject came in 1957, when he was awarded a Senior Postdoctoral Fellowship from the National Science Foundation.[51] During his fellowship year Odum spent time at the Nevada Proving Grounds and at the nuclear facility at

Hanford, Washington. This experience provided him with the background to write the chapter on radiation ecology.

Odum's discussion of radiation ecology was perhaps the first review of the subject directed toward a general audience. Its appearance was quite timely. By the mid-1950s there was widespread public concern about the effects of low-level radiation in the environment. The United States, the Soviet Union, and Great Britain continued to test weapons in the atmosphere, and the controversy over "fallout" increased public awareness of radiation. Scientists were divided on the issue. The geneticist H. J. Muller, who was awarded the Nobel Prize in 1946 for his demonstration of the mutagenic properties of x-rays, warned against "race poisoning" from nuclear tests.[52] According to Muller even an extremely small increase in the mutation rate would eventually lead to a significant "genetic load" on the human genome. Muller's claim was highly controversial, but other prominent geneticists also voiced concerns about potential dangers of fallout for individuals and populations. Ecologists also responded to the problem, but from a slightly different perspective. After Hiroshima and Nagasaki, the American public could easily imagine the deleterious genetic and physiological effects of radiation. Less obvious, but no less ominous, were environmental effects. Ecologists, therefore, could present radiation in the environment as a pressing social and scientific issue, one that was poorly understood. At the same time they could use the problem as a justification for government support of what they considered an exciting line of research.

In his chapter on radiation ecology, Odum discussed the fallout problem briefly, but minimized the general risk to human health or the environment. For Odum, two other problems were more worrisome: biological magnification and nuclear waste storage. Researchers at the Hanford nuclear facility had recently discovered that radionuclides discharged into the Columbia River in trace amounts sometimes became greatly concentrated as they moved through the food chain. For example, the concentrations of radioactive phosphorus (^{32}P) were often hundreds or thousands of times greater in vertebrates at the ends of aquatic food chains than in the cooling water leaving the nuclear reactors. The potential danger from biological magnification seemed obvious. As Odum pointed out, "we could give 'nature' an apparently innocuous amount of radioactivity and have her give it back to us in a lethal package!"[53] The phenomenon of biological magnification later became more closely identified by the public with the problem of pesticides in the environment. Rachel Carson's *Silent Spring*, published three years after the second edition of Odum's textbook, made this a cause célèbre for the popular environmental movement.[54] But Odum and other radiation ecologists were less alarmist in their attitude toward the biological magnification of radionuclides. The actual danger of biological magnification depended upon a number of variables including the half-life of the nuclide, the ability of organisms to retain the element, and the concentration of the nonradioactive isotopes of the element in the environment. Furthermore, the phenomenon of biological magnification opened up new opportunities for ecosystem research. Because certain radionuclides accumulated in the various trophic levels of an ecosystem, tracer studies could determine the flow of energy and materials through the system. Thus, Odum concluded, "Man's opportunity to learn more about environmental processes through the use of radioactive tracers balances the possible troubles he may have with environmental contamination."[55]

Disposal of radioactive waste was a far more troubling problem for Odum. Like the emotional debate about fallout, concerns about waste treatment and disposal had become a controversial public issue by the time Odum revised his textbook.[56] The Atomic Energy Commission had a twofold policy on waste disposal. For low-level waste, the policy was "dilute and disperse." Liquid wastes underwent preliminary treatment to reduce radioactivity, and then they were released into waterways. Solid wastes were buried or dumped into the ocean. The AEC was convinced that this method of disposal was both safe and environmentally harmless. Because there was no satisfactory way to dispose of high-level nuclear waste, the AEC policy was "concentrate and contain." By 1957 highly radioactive liquid waste from the nation's reactors amounted to sixty-two million gallons, most of which was stored in underground tanks at Hanford, Washington. This temporary storage was to be superseded at a later date when suitable means of permanent disposal were developed. But by the time that Odum wrote his chapter on radiation ecology the tanks were already beginning to leak.

A number of scientists publicly voiced concerns about both aspects of the Atomic Energy Commission's disposal policy.[57] Odum's chapter reflected these misgivings. He admitted that the nine billion gallons of low-level radioactive waste entering the environment each year constituted a mere "drop in the bucket" compared to the vast volume of the oceans.[58] Nonetheless, Odum warned that the environmental impact of low-level waste might become critical late in the century if nuclear power became a major source of energy. The proliferation of reactors and the economic incentives to minimize the cost of waste treatment would inevitably lead to greater environmental contamination. Moreover, the possibility of biological magnification meant that even the limited discharge of low-level wastes into waterways was not necessarily harmless.

The problems that Odum stressed in his chapter on radiation ecology were not the evolutionary, population-level problems raised by geneticists such as H. J. Muller. Rather, they were ecosystem problems involving complex interactions of both abiotic and biotic components. Odum concluded that these problems were not yet critical in 1959, but that they might become critical in the near future. Therefore, solving these problems served as a compelling justification for expanding ecological research, specifically the type of ecosystem studies that Odum had been pioneering. Some ecological interactions could be studied in the laboratory. Ultimately, however, the fate of radionuclides in the environment could only be understood through experiments on natural ecosystems. "In the not too distant future," Odum concluded, "the radioecologist may well be one of those who must help decide when to contain and when to disperse the waste materials of the atomic age. If the ecologist does not know what to expect in the biological environment, who will?"[59]

A Symbiotic Relationship

At the beginning of this chapter I characterized the relationship between ecosystem ecology and atomic energy as symbiotic. From an evolutionary viewpoint, symbiosis implies more than mutual benefit. The boundaries between cooperation and competition, parasitism and mutualism are often poorly marked and easily crossed. Altruism may not reflect good will, but simply self-interest in disguise. Social symbiosis is no less complex and ambiguous than its biological model. Such is the case with ecosystem ecology in the atomic age.

The nascent ecological specialty that emerged from World War II clearly benefited from the rise of atomic energy. As we have seen, radionuclides provided ecologists with a new set of exotic tools and new research opportunities. In the Atomic Energy Commission ecologists found a rich source of financial support, and in public concerns over the effects of radiation they found a convincing justification for their new lines of research. By embracing atomic energy were ecosystem ecologists motivated by nothing more than self-interest? And why should the atomic energy establishment have taken interest in a still rather insignificant scientific specialty struggling to establish itself?

Certainly one cannot entirely rule out environmental concerns as part of the answer to the second question. The AEC had a dual mandate; the agency was established in 1946 both to promote and to regulate the development of atomic power.[60] As critics pointed out, regulation usually took a back seat to promotion, but in its regulatory capacity, the agency relied upon the technical input from scientists, including ecologists. Even at the height of World War II, there had been concerns about the environmental impact of atomic energy. During the construction and early operation of the nuclear facility at Hanford, high officials of the Manhattan Project had authorized limited environmental studies.[61] And extensive biological and geological surveys were part of Operation Crossroads, the first postwar atomic tests at Bikini Atoll. Nonetheless, I think that it is safe to say that concern for the environment was never the principal rationale for supporting ecological research. If it had been, the AEC would probably have supported a complete preoperational environmental study of the Savannah River site in 1951, rather than providing Eugene Odum with only modest funds to survey animal populations near the new reactors. But if concern for the environment was only a small part of the equation, then what was the government's primary rationale for supporting Odum and other ecosystem ecologists?

In her stimulating book, *A Fragile Power*, Chandra Mukerji argues that the state is less interested in specific technical information that scientists generate than in their broader technical expertise.[62] The scientific community, in Mukerji's view, constitutes an elite reserve labor force. The state supports scientific research, even research with little apparent practical application. In return, the state gets a pool of highly trained problem solvers. Developing such a pool of experts was a major priority of the government immediately after the war.[63] Funding basic research in ecology may have supplied a means for generating technical information and allowed ecologists to pursue research they found exciting, but in addition it provided the government with the means for training a cadre of experts knowledgeable about ecology and the environmental effects of radiation.

There is more to Mukerji's thesis than this, for she claims that the state uses science to legitimate its policies. One need not accept this thesis in all its details to apply it to the case of atomic energy. Ecologists and other scientists provided the AEC with technical information about the effects of atomic energy. But this information was often ambiguous, even contradictory, and often enough it could be used to criticize AEC policy.[64] The fact that policy makers in the AEC used this technical information selectively and sometimes misled the American public about the potential dangers of fallout should not obscure the important legitimizing role that scientists played in this process.

The AEC, supporting research on a grand scale, was apparently using scientific data in the decision-making process. By doing so, this controversial federal agency could cloak itself with the cultural authority of science. This was particularly true after the Eisenhower administration launched its Atoms for Peace program in 1953.[65] The program was an attempt to build public support for atomic energy in the wake of the first hydrogen bomb tests. It was also designed to put the Soviet Union on the defensive in terms of worldwide propaganda. One cornerstone of Atoms for Peace was support for basic research, specifically the use of radioisotopes as tracers. Tracer methodologies were sufficiently novel that the AEC isotope program attracted a great deal of interest from elite scientists, including ecologists. At the same time, the government used the program to publicize its commitment to the peaceful uses of atomic energy.

Mukerji presents a rather bleak picture of modern science. Scientists have exchanged independence and cultural legitimacy for financial support from the state. If so, it must be said that after some initial concerns and skepticism, few scientists showed much enthusiasm for returning to prewar patterns of research. But what were the motivations of ecosystem ecologists during the critical period of transition after World War II? Were they, to paraphrase a later critic, seduced by new economic opportunities?[66] Given our late twentieth-century biases cultivated by post–Vietnam War skepticism toward authority, the debacles at Three Mile Island and Chernobyl, and the recent revelations about safety violations at Hanford and Savannah River, there is a great irony in Eugene Odum, "Mr. Ecology," working so closely with the nuclear arms industry.[67] But his situation was hardly unique. Even the geneticist H. J. Muller, perhaps the most outspoken scientific critic of atomic energy policy, turned to the AEC for financial support. During the opening days of the Cold War few doubted the need for some nuclear deterrence. And behind this dark cloud there appeared to be a silver lining. For scientists and AEC administrators alike, nuclear technology promised a "scientific renaissance."[68] The delight of making new discoveries seemed impossible to resist. There was an almost universal optimism that the potential benefits of atomic energy outweighed its destructive power, that nuclear swords could eventually be beaten into plowshares. As AEC historians Richard Hewlett and Jack Holl conclude, "To bring that hope to reality was a strong and uplifting motivation."[69]

The ambiguities of the new relationship between science and the state were not entirely lost upon those who forged it. In his famous farewell address, an address in which the term "military-industrial complex" was coined, Dwight Eisenhower warned that the ideals of science might be perverted by the political process.[70] There was also the danger that science, as a partner in this new complex, might work to subvert democracy. Ecologists, too, sometimes ruminated on their new partnership with government. For Eugene Odum, nuclear technology was always a double-edged sword. Although confident that potential benefits outweighed environmental costs, he was forced to admit that a quarter century after Hiroshima, atomic energy remained primarily a military technology.[71]

7

The New Ecology

Ecologists can rally around the ecosystem as their basic unit just as molecular biologists now rally around the cell.

—Eugene P. Odum, "The New Ecology"

By 1964 Eugene Odum was proclaiming the arrival of a "new ecology" that took the ecosystem as its fundamental object of study.[1] This new ecology was deeply rooted in historical tradition, but, as Odum acknowledged, its rapid rise owed much to atomic energy and other postwar developments. Odum and his younger brother Howard were at the center of this emerging specialty. Their award-winning research served as a model for early ecosystem studies. Together they pioneered the teaching of ecosystem ecology with advanced courses for college teachers at the Marine Biological Laboratory at Woods Hole (1957–1961). And they wrote the first textbook organized around the ecosystem concept. Eugene Odum's *Fundamentals of Ecology*, partly written by his brother, went through three editions (1953, 1959, 1971) and was translated into more than twenty languages.[2] No other textbook had such a profound influence upon the teaching of ecology during the 1960s; as one critic grumbled, for nearly twenty years the "odum" was the unit by which the success of ecology textbooks was measured.[3]

An Unusual Team

Eugene Odum was born in 1913, the son of the prominent sociologist Howard Washington Odum. The elder Odum was best known for his writings on American regionalism, the changes in southern society, and the effects of technology on social order. But he was also the scion of a strong tradition of organicism in American sociology. He apparently was an important influence upon his son's thinking, a man whose ideas Eugene would refer to again and again in his writings. Undoubtedly from his father Eugene inherited his commitment to organic holism, looking at the big picture in ecology.[4] This holistic approach was deepened and strengthened while he was a graduate student in zoology at the University of Illinois.

Odum entered the graduate school at a particularly exciting time. The chairman of the zoology department, Victor Shelford, was completing the manuscript of *Bio-Ecology*, a book coauthored with Frederic Clements. The book, though not a critical success, did provide the strongest statement of the organic point of view long championed by both authors. Odum's adviser, the young physiological ecologist Charles Kendeigh, also held some Clementsian ideas. However, the dissenting views of Henry Allan Gleason were also being taught, particularly by the plant ecologist Arthur Vestal. And Arthur Tansley's ecosystem paper appeared only two years before Odum arrived. Therefore, graduate students were exposed to a cross fire of ideas about the fundamental units of ecology.[5] Odum's dissertation, an experimental study of the heart rates of birds, may appear far removed from such theoretical concerns, but his interests in physiology and ecology meshed perfectly.[6] As Odum later recalled, "The transition from bird physiology to ecosystem function was quite natural for me since it involved moving up the hierarchy from physiological ecology of populations to the physiological ecology of ecosystems. It's really not such a big step to go from whole organism metabolism to community metabolism."[7] This physiological perspective became a hallmark of Odum's research.

The actual transition to ecosystem research came as a result of Odum's work for the Atomic Energy Commission, but it was stimulated by his brother who was completing a Ph.D. under G. Evelyn Hutchinson. During the late 1940s Howard was sending his older brother copies of Hutchinson's lecture notes, and Eugene himself was corresponding with the Yale limnologist.[8] Thus, *Fundamentals of Ecology* reflected a strong Hutchinsonian influence, particularly with respect to energetics and biogeochemical cycling. This influence was most noticeable in the chapter on energy that Howard contributed to the book, but looking back on this period Eugene also emphasized the degree to which his own early ideas on ecosystems were shaped by Hutchinson.[9]

Some of Eugene Odum's ideas have been controversial, but he has always remained within the broad mainstream of professional ecology. In contrast, Howard has cultivated an image as the enfant terrible of ecology, a specialist in unpopular ideas.[10] Controversy has followed him throughout his career. Nonplussed by a rather speculative introductory chapter in his dissertation on strontium cycling, Odum's graduate committee strongly recommended that Hutchinson remove the "philosophical vagaries" from his student's work. Hutchinson refused, and the dissertation retains its idiosyncratic fusion of biogeochemistry and evolutionary theory.[11] This episode, in 1950, foreshadowed what would become a somewhat stormy career. Controversy notwithstanding, Odum's image as an ecological outsider is a bit contrived. In attracting funding and graduate students he has had a remarkably successful career. Together with his older brother, he has been the recipient of prestigious scientific awards.[12] And his ideas have had a profound impact upon ecology, although sometimes indirectly through the writings of Eugene. But the fact that the older brother is perceived as a mainstream ecologist while the younger is perceived as a maverick reflects more than differences in style and personality. It also reflects subtle, but important, differences in the way the two men view nature. If Eugene has approached ecosystem ecology like a physiologist, then Howard has always approached nature like a physical scientist or engineer.

Like his brother, Howard emphasizes the important formative role that his father played in his intellectual development. His boyhood interests in biology were stimulated by Eugene, who was eleven years his senior, and by the ichthyologist R. E. Coker, for whom he worked after school. Unlike his brother, Howard was always strongly attracted to the physical sciences. As a youth he dabbled in electronics, a nascent interest that later found serious expression in his computer simulations of ecosystems.[13] During World War II he served as a meteorologist in the Air Force. As he later recalled, this experience with complex, large-scale natural phenomena taught him to appreciate the need to study systems holistically.[14] It also provided him with an entree to the biogeochemical research that he pursued as a graduate student.

Odum was introduced to Hutchinson through his father who was a visiting scholar at Yale after the war.[15] It was a propitious time to work with the limnologist, for his research program was approaching its zenith. Hutchinson, who was then participating in the Macy conferences on cybernetics, was attempting to complete a formal synthesis of biogeochemistry and population ecology. As a result, he was attracting an unusually diverse group of very bright graduate students. The grand synthesis never occurred, and his students all moved toward one pole or another; but during the late 1940s the intellectual environment around Hutchinson was extremely stimulating.

Odum attended one Macy conference with Hutchinson, an event that impressed him only by its confusion and lack of intellectual clarity; however, Hutchinson's paper, "Circular Causal Systems in Ecology," which was a product of the conferences, served as a model for Odum's early work. Even more influential was Alfred Lotka's, *Elements of Physical Biology*, a book that Hutchinson recommended to his student.[16] Published in 1925, Lotka's book attempted to define a new area of biological research: physical biology. Physical biology was to be the application of physical principles to complex biological systems, particularly that all-encompassing system that we now refer to as the biosphere. From Lotka's perspective, that of the physical chemist, all biological processes could be reduced to exchanges of matter and energy among the compartments of a system. As such, biological systems were governed by the laws of thermodynamics. But biological systems differed in two important ways from the type of closed chemical systems traditionally considered in thermodynamics. They were more complex, and, unlike isolated chemical systems, they were open to continuous inputs and losses of energy. Therefore, biological systems never came to a true equilibrium state, defined in terms of maximum entropy, but rather attained a steady state, defined in terms of constant energy flow. Lotka's ideas on energy flow were not widely adopted by ecologists during the 1920s and 1930s, but particularly through the writings of Howard Odum they had a pervasive influence upon the way later ecologists thought about ecosystems.

The ideas of open systems and steady states could be applied very broadly in biology. Energy transfer associated with predation and the cycling of elements were obvious cases. But Lotka also used his open systems approach to discuss population dynamics in kinetic terms, where the size of the population was a function of the constant entry and removal of individuals. This general approach was later expanded upon by Hutchinson and some of his students. Less propitiously, Lotka also attempted to explain evolution in thermodynamic terms. Evolution, for Lotka, was not so much species changing over time, but rather the overall accumulation and distribution of energy within a system. Natural selection always maximized the flow of energy and matter through this system. This curious idea seems to have been almost completely ignored by more traditional evolutionary biologists. Referring to it as the "maximum power principle," Odum made it the leitmotif of his controversial evolutionary writings.

By the time that Odum was a graduate student, steady state thermodynamics was attracting considerable attention in scientific circles.[17]

Hutchinson encouraged his students to explore this literature, and the ideas, particularly Lotka's, were widely discussed among the Yale ecologists. Given his background in the physical sciences, particularly his training in meteorology and physical chemistry, it is perhaps not surprising that Odum should have been so attracted to Lotka's book. As Peter Taylor has pointed out in a perceptive article, Lotka had a much greater influence upon Odum than he did on more biologically oriented ecologists.[18] Whereas Hutchinson and others only borrowed Lotka's mathematical models, Odum fully grasped the intent of Lotka's physical biology. More than almost any other ecologist, he has approached the study of ecosystems as a physical scientist might. As we shall see, this approach often brought him into conflict with other biologists, particularly more traditional evolutionary ecologists.

Within months after defending his dissertation, Howard Odum was writing the chapter on energetics for his brother's textbook. Together the two made an unusual team. In terms of personality, scientific style, and intellectual perspective they were very different, and during the years when they were establishing the "new ecology" there was a bit of sibling rivalry. In important ways, however, their talents complemented one another. The success of *Fundamentals of Ecology* reflects this fruitful collaboration. One can trace much of the evolution of the ecosystem concept through the subsequent editions of the textbook. It not only presented the ideas of the two Odums as they developed over two decades, but the textbook also provided a synthesis of ideas from other leading ecosystem ecologists. One of Eugene Odum's most important skills has been his ability to make often abstruse theory intelligible to a general audience. As a result, what might have remained part of a rather narrow, technical literature was brought into the mainstream of biological thought. Among ecosystem ecologists he may not have been the most original thinker, but through his semi-popular writings Eugene Odum was easily the most influential. For admirers and critics alike, the name Odum became indelibly linked with ecosystem ecology.

A Refined Concept

It is useful to think of scientific concepts as modular constructs. The parts fit together to form a more or less unified whole, but some parts can be removed or replaced without destroying it. As a concept becomes refined, original ideas may even be replaced by their contradictories.[19] Such is the case with the ecosystem concept as it evolved during the 1950s and early 1960s. Nearly all ecologists accepted some key components, although the scientists might interpret them slightly differently. Some original ideas were abandoned or replaced by quite different ones. Other components remained unsettled. One could conceivably reject one or more of these and still be an ecosystem ecologist. What follows is a kind of conceptual map of these ideas.

The Machinery of Nature

Two of Tansley's conceptual innovations remained at the core of ecosystem ecology. Unlike population and community, which were exclusively biological, the ecosystem was the one commonly used ecological concept that encompassed both biotic and abiotic factors. As such, it was a particularly useful term for discussing biogeochemical cycles and energy flow. It also became useful for discussing many practical environmental problems that could not be clearly demarcated along biological and nonbiological lines. Rival terms, such as biogeocoenosis, never gained much of a following outside the Soviet Union. Tansley's notion that systems are defined by the investigator also proved to be a durable innovation. Ecologists had long bickered about the natural boundaries of plant and animal communities. For most ecosystem ecologists, such arguments were both fruitless and irrelevant. The ecosystem was not so much a concrete geographical entity as a flexible abstraction. An ecosystem such as a small pond was not completely isolated from its surroundings. Although its boundaries might be poorly marked, the investigator could still define it as a "system" for the purpose of ecological study. Energy, chemical substances, or organisms might regularly move in and out of the system, but these movements could be treated as simple gains and losses in the ecosystem budget. The flexibility that this allowed in pursuing studies of energy flow and material cycling was very attractive, and this original idea was also widely accepted by later ecologists.

Some of Tansley's other ideas changed, but in subtle ways. The term *ecosystem* had arisen out of Tansley's critique of Clementsian ecology. Despite his fascination with the philosophy of modern physics, neither Tansley nor later ecosystem ecologists, ever completely abandoned Clements's organismal metaphor, although after World War II, there was what Peter Taylor describes as a "partial transformation" of ecological metaphors, a gradual shift from organic to machine images.[20] One might, for example, contrast the organismal allusions in Raymond Lindeman's trophic-dynamic paper with

George Clarke's postwar picture of the ecosystem as a set of interlocking gears.[21] Of course, the notion that something can be both organism and machine is not unusual in biology. And the postwar development of cybernetics, in which ecology took part, encouraged analogies between the industrial and organic worlds.

The Odums's writings exemplify this januslike conception of ecosystems. Eugene Odum, trained within a basically Clementsian tradition, has always stressed the organismal attributes of ecosystems: development, metabolism, and homeostasis. Ecosystems are not, in fact, organisms, although one can draw useful parallels between them.[22] For example, when he needs an analogy for communication and control mechanisms in the ecosystem, Eugene turns to the physiology of the endocrine system.[23] For Howard Odum, ecosystems are only very complex machines. Processes in ecosystems are fundamentally no different from those of water wheels, steam engines, and electrical circuits. Writing in 1959, he stated, "The relationships between producer plants and consumer animals, between predator and prey, not to mention the numbers and kinds of organisms in a given environment, are all limited and controlled by the same basic laws which govern non-living systems, such as electric motors and automobiles."[24] When Howard Odum speaks of communication and control, he rarely turns to organic analogies; instead, he speaks of the invisible wires in nature's circuits.[25]

The complementarity of these images is most evident in the Odums's writings on self-regulation and the steady state. Ideas of stability and self-regulation permeate the writings of both Odums, going back to their Ph.D. dissertations. Beginning with the second edition of *Fundamentals of Ecology* (1959), Eugene Odum began discussing these phenomena explicitly in terms of homeostasis.[26] He had read Walter B. Cannon's *The Wisdom of the Body* as a graduate student during the late 1930s, and he later used it as required text in the physiology course that he taught at the University of Georgia.[27] Cannon's concept of homeostasis—the idea that organisms are capable of maintaining internal stability in a fluctuating environment—was directly applicable to Odum's early research in physiological ecology. But Cannon's approach also held more general appeal for Odum who shared the Harvard physiologist's commitment to functionalism, the holistic study of complex biological systems, and the close analogy between biological and social entities.[28]

For Odum, homeostasis became a general biological principle. Homeostatic mechanisms acted at all levels of biological organization from cells to ecosystems. Thus, Odum was not simply reformulating the Clementsian argument that the ecosystem is a kind of organism because it is homeostatic. Rather he was making the much stronger claim that all living systems—cells, organisms, populations and ecosystems—share this common self-regulatory property. Part and parcel of this way of looking at the living world is the acceptance of biological functionalism. For Odum, individual organisms and populations really are *parts* of the ecosystem in the sense that they carry out particular functional roles. Individuals might compete with one another, but if an ecosystem is to survive, competition must be balanced by cooperation. Thus, the evolution of stability in ecosystems occurs through a reduction in competition and an increase in mutualism. For example, Odum would like to see the evolution of lichens as a progressive change—from the primitive condition where a fungus parasitizes its algal host to a truly mutualistic association where both fungus and algae benefit. "Like a balanced equation," Odum wrote, "it seems reasonable to assume that negative and positive relations between populations eventually tend to balance one another if the ecosystem is to achieve any kind of stability."[29]

Odum believed that the evolution of homeostasis and the consequent stability of ecosystems occurred through a combination of group selection and coevolution. By the late 1960s such statements were highly controversial, but during the 1950s they reflected mainstream biological thought. As Gregg Mitman has described in his detailed study of ecology at the University of Chicago, Alfred Emerson had been expressing similar ideas about homeostasis and evolution for more than a decade.[30] Odum was familiar with Emerson's work on social insects and may have derived some of his ideas from it. But the concept of homeostasis was being used so widely after World War II that tracing lines of influence is difficult. During the two decades following the war, a diverse group of scientists used homeostasis to explain a broad range of biological phenomena.[31]

In contrast to his brother's more biological account of ecosystem stability, Howard Odum attempted to provide a thermodynamic explanation. Citing Lotka's *Elements of Physical Biology*, he argued that natural selection favored those systems that maximized power output in the form of growth, reproduction, and maintenance. But maximum power required a sacrifice in efficiency. Using the example of Atwood's machine, a simple system composed of two weights connected by a rope attached to a pulley, Odum noted that maximum power output is attained at 50 percent efficiency. In short, the optimum efficiency for power production was much less than maximum efficiency. This "maximum power principle," Odum believed, applied not only to simple laboratory demonstrations but to all systems, including the complex open systems of the biological world. Power was at a premium in the struggle for existence, but it was not the only factor for survival. Natural selection favored not only the most powerful systems but also the most stable. This "stability principle," which Odum attributed variously to Lotka and the University of California zoologist Samuel J. Holmes, stated that as living systems evolve, increasing amounts of energy are diverted to maintenance.[32] In a climax ecosystem, like the coral reef at Eniwetok Atoll that he and his brother had studied, nearly all the energy trapped by the producers was used to maintain the complex living community. "As an open system," he wrote of the reef, "the construction of self-regulating interactions has led by selective process to the survival of the stable."[33] Such stable ecosystems were in a thermodynamic steady state; photosynthesis was almost completely balanced by respiration.

The maximum power principle and the stability principle could be easily translated into the language of homeostasis. Walter B. Cannon made an important observation in *The Wisdom of the Body:* organisms often sacrifice efficiency to maintain stability. Large amounts of energy are used to maintain the proper balance of water and minerals in the body.[34] Although this might appear uneconomical, Cannon believed that homeostatic stability was a necessary precondition for the evolution of the vertebrates. This fusion of physiological and physical metaphors for ecosystem stability became even tighter during the 1960s when the language of cybernetics began to enter ecology. Cybernetics, as originally conceived by Norbert Wiener, had drawn heavily upon Cannon's physiology, but after the war many biologists used cybernetics as a new way to discuss organic self-regulation. For Howard Odum, feedback loops in ecosystems could be diagrammed as if they were parts of an electronic circuit. For Eugene Odum, these loops were more closely analogous to hormonal or neural control systems. But as his later writings suggest, homeostasis and cybernetics were simply two different ways of discussing the same thing.[35]

Systems Thinking and Systems Ecology

Cybernetics was just one example of a broader intellectual movement that developed after World War II, a development that Robert Lilienfeld has referred to as "systems thinking."[36] New areas of research such as cybernetics, general systems theory, operations research, game theory, information theory, and computer simulation were premised upon the belief that diverse physical, biological, and social entities could be treated as systems. In his highly critical history, Lilienfeld identifies two related characteristics with the rise of systems thinking. One is *syncretism,* the tendency for what were once distinct technical disciplines to fuse. Many supporters of systems thinking advocated interdisciplinary sharing; indeed, they often saw systems theories as tools for breaking down disciplinary barriers. The other characteristic is *migration,* the movement of systems thinking into previously well-established disciplines. This migration can take the form of technical innovation, but, according to Lilienfeld, it is also characterized by missionary essays, programmatic statements, and the rhetorical use of technical jargon.[37] Systems Ecology, a term coined by Eugene Odum, partook of both syncretism and migration.[38]

Historians have emphasized the difficulty of adequately defining systems ecology.[39] This might be expected in a case where several scientists more or less independently borrowed from an already heterogeneous mix of ideas; however, the situation is not entirely chaotic. For the purposes of this discussion, I identify three broadly overlapping definitions of systems ecology. In a very general sense, ecosystem ecology and systems ecology could be used as synonyms. Systems ecology could be much more narrowly identified with the small, highly technical subdiscipline of ecosystem modeling. Finally, one might identify systems ecology with Howard Odum's ambitious and idiosyncratic attempt to create a universal science of systems.

The general use of the term is best exemplified by the work of Eugene Odum. For him, systems ecology was as much a "state of mind" as it was a set of mathematical techniques.[40] It involved thinking about the living world in the way Arthur Tansley had suggested during the 1930s. The philosophical core of Tansley's ecosystem concept was the belief that nature is composed of innumerable, partially overlapping systems. These spatiotemporal units could be of any size; an ecosystem might be an aquarium, a space capsule, a farmer's field, a pond, or the entire biosphere.[41] Thus, to be an ecosystem ecologist required one to think in terms of systems; as Odum succinctly put it, "the new ecology is thus a systems ecology."[42] Odum often borrowed from the language of cybernetics and other systems sciences to discuss ecological phenomena. For example, the idea of negative feedback control could be used interchangeably with the more biological idea of homeostasis. But this was borrowing, or, to use Lilienfeld's metaphor, it represented the migration of cybernetic ideas into the established discipline of ecology. There is little evidence that Odum himself delved deeply into the technical literature of cybernetics or systems theory.

Significantly, when it came time to prepare the third edition of *Fundamentals of Ecology*, the new chapter on systems ecology was written not by Odum, but by the younger biologist Carl J. Walters.

If systems ecology could be used synonymously with ecosystem ecology, then it could also be identified with a much smaller subspecialty that began to emerge during the early 1960s. For ecologists such as Ramon Margalef, Howard Odum, Jerry Olson, Bernard Patten, Lawrence Slobodkin, George Van Dyne, and Kenneth Watt, systems sciences offered an array of new tools for dealing with complexity. "The significant features of the approaches," Patten wrote, "are that they are essentially mathematical in nature, and they require modern computing equipment for effective application."[43] For Patten and others, the ecosystem might be a "keystone" concept, but it was one that could be explained fully only in the language of mathematics. This smaller group of "systems ecologists" was distinguished by two important characteristics. In contrast to Eugene Odum, for whom systems thinking was primarily qualitative, this group more fully exploited the technical innovations of the systems sciences. And rather than simply borrowing systems thinking, these ecologists contributed to the journals and interdisciplinary conferences that had sprung up around the new systems sciences. They were enthusiastic proponents of what Lilienfeld refers to as the syncretism of systems thinking.

If systems ecology involved the migration of new ideas into an established discipline, this was not accompanied by a migration of scientists. Almost without exception, the systems ecologists were trained in traditional biological programs.[44] Typical of this group was Bernard Patten. As an undergraduate zoology major at Cornell, Patten took no courses in mathematics. He began working on a master's degree in botany at Rutgers University in 1954 but was inducted into the Army. While doing pesticide research at Fort Detrick, Maryland, he was introduced to a series of essays on the use of information theory in biology. He later recalled that his inability to follow the mathematics made the essays all the more intriguing.[45] Once he had "caught the systems bug," Patten read widely in the literature of the systems sciences, and he took several courses in mathematics as he completed his Ph.D. His dissertation used information theory to measure the diversity of a phytoplankton community.

As a young professor at the College of William and Mary, Patten assigned Ross Ashby's *Introduction to Cybernetics* as a textbook in his marine ecology course. Taught during the early 1960s, this may have been the first course in "systems ecology." But the real development of the subspecialty came when Patten moved to the Oak Ridge National Laboratory in 1963. The laboratory, with its heavy emphasis on the physical sciences, had the advanced computers needed for sophisticated modeling, and two other biologists on the staff shared Patten's enthusiasm for systems ecology: Jerry Olson and George Van Dyne.

Like Patten, both Olson and Van Dyne came from traditional biological programs. Olson received a Ph.D. in botany from the University of Chicago in 1951 with a dissertation on soil changes during dune succession. Often compared favorably to Cowles's classic study of the same dunes, Olson's doctoral research won the prestigious Mercer Award from the Ecological Society of America. Van Dyne was the product of an agricultural program. He had a bachelor's degree in agriculture from Colorado A & M College and a master's in animal husbandry from South Dakota State University. His Ph.D. was in nutrition from the University of California at Davis with a dissertation on the effects of cattle grazing on grassland ecosystems. Although interested in ecological modeling, Van Dyne had little experience with computers before he arrived at Oak Ridge.

Olson was the first of the three to arrive at Oak Ridge. By 1960 he was continuing his soil studies with the use of radioactive tracers and experimenting with the use of analog computers to simulate ecosystems. He was perhaps the first ecologist to do so. Patten arrived at Oak Ridge in 1963, followed a year later by Van Dyne. The interests and abilities of the three ecologists apparently complemented one another. Patten later recalled that his experience at Oak Ridge was exciting, even exuberant.[46] Funded by grants from the Ford Foundation and the National Science Foundation, the group offered an advanced course in systems ecology through the nearby University of Tennessee. Although it was intended primarily for graduate students, the course was audited by a number of postdoctoral fellows, visiting scientists, and faculty members.[47] This fruitful collaboration was short lived. By 1968 both Patten and Van Dyne had moved back to academia. But the team had left its mark: after 1968 Oak Ridge was recognized as the leading center for systems ecology in the United States.

Systems ecology was as diverse as the systems sciences that it drew upon, but at the core of this enterprise was the use of computers for modeling and simulation. Increasingly, the new digital computers were used for this purpose. Van Dyne, who had learned FORTRAN programming, had already begun to explore its possibilities during his brief stay at Oak Ridge. But the early development of systems ecology relied more heavily upon analog computers. In an analog computer electrical circuits are used to represent the features of the system under study. More to the point, the circuits represent mathematical equations describing these features. During a simulation, the computer generates voltages that behave like the mathematical variables in the equations. In this way several equations can be solved simultaneously. For the systems ecologist, analog computers served two important purposes.[48] They could be used to model very large, complex systems. Physical and biological processes occurring over the course of several decades could be rather quickly simulated in the laboratory. This had tremendous theoretical and practical implications for predicting the behavior of real ecosystems. But the very process of building analog models also played an important heuristic function. Modeling involved a stepwise process of abstraction from the complexity of nature to the relative simplicity of the analog circuitry. For example, the ecologist might identify and isolate food chains within an ecosystem, draw compartment diagrams representing the flow of energy through these chains, write mathematical equations representing the rates of energy flow, and finally create the analog program (i.e., circuit diagram).[49] This process of abstraction could be a powerful stimulant for the scientific imagination, leading to new questions about the real system under study. In a more general way, systems ecology could also serve as a "strategy of research," a set of procedures that forced the ecologist to keep the "big picture" in mind.[50] By building models explicitly in terms of systems and component subsystems, one might hope to achieve a coherent explanation, rather than a collection of fragmentary results.

There is no reason why the type of systems ecology described above should necessarily be restricted to the study of ecosystems, and, in fact, ecologists such as Kenneth Watt and C. S. Holling used systems analysis to study populations. Thus, there is some justification for claiming that systems analysis has become a standard tool in ecology.[51] However, for better or worse, systems ecology and ecosystem ecology became closely linked. When supporters, and especially critics, spoke of systems ecology, they were usually speaking within the context of ecosystem studies. Partly this was a result of Eugene Odum's "missionary essays" that equated the two. Partly it was owing to the boost that both ecosystem ecology and systems ecology received from the International Biological Program (discussed in chapter 9). Partly, it was also responding to the way that Howard Odum used both the ecosystem concept and systems ecology in his attempt to build a grand systems science.

Independent of the Oak Ridge group, Howard Odum also experimented with analog models of the ecosystem during the early 1960s. He and his students published a number of important modeling papers, including two in the high visibility journals *Science* and the *American Scientist*.[52] But he was hampered by a lack of sophisticated computer equipment, and thus he turned to a more conceptual approach to systems ecology. In early analog models, ecological variables were simulated by actual electronic components such as resistors and capacitors; however, by the end of the 1960s these were replaced in Odum's circuit models by a more general set of energy symbols. From Odum's perspective this new approach had important advantages.[53] It freed him from some physical restrictions imposed by electrical circuits, and it allowed him to develop a universal energy language (*energese*) for modeling systems, in general. Odum believed that this language could be applied to any system: electrical, mechanical, biological, or social. This ambitious program in systems ecology was summarized in Odum's semipopular book, *Environment, Power, and Society* (1971).

Odum's book, an eclectic and idiosyncratic work aimed at a general audience, was intended to explain basic concepts in ecology using Odum's energy language.[54] The early chapters provided an excellent summary of ecosystem ecology and a coherent introduction to systems modeling. It also presented a cogent argument for the limits of industrial growth. Circuit diagrams were skillfully used to illustrate the dependence of agricultural ecosystems and industrial societies upon fossil fuel subsidies. Left at that, the book might have become one of the most important environmental treatises of the 1970s. Less auspiciously, in later chapters Odum applied his systems approach to politics and religion. "The energetic laws are as much first principles of political science as they are first principles of any other process on earth," he claimed.[55] Voting, public opinion, taxes, even revolution and war could be expressed in the language of energy circuits. This large-scale reduction of complex social phenomena to simple quantitative variables exemplified one of the "besetting vices" that Lilienfeld has identified with systems thinking.[56] Lilienfeld complains that by mechanizing human behavior and social interactions, systems thinking inevitably leads to authoritarianism. Odum's book is a case in point. Although he claimed to be defending democracy, the simple control loops of his energy diagrams were more suggestive of coercion and manipulation than of individual freedom.

Odum's excursion into social and political discourse was unfortunate. *Environment, Power and Society*, with its penetrating insights into environmental problems, might have been influential, but apparently it was not taken seriously by professional ecologists. Book reviewers in many leading journals read by ecologists simply ignored the book. The review in *Science,* although not entirely hostile, emphasized the idiosyncratic character of Odum's systems thinking. Egbert Leigh, another student of G. Evelyn Hutchinson, praised Odum for undertaking such an ambitious project, but then he added that the book was "a most maddening work, which at first sight seems totally undisciplined, a chaotic mixture of the asinine, the banal, and the brilliant, with random observations, often in conflict with the available evidence, on nearly everything under the sun."[57] Unfortunately, Odum seemed to be repeating the fate that had befallen his intellectual model, Alfred Lotka, a scientist who never successfully reached his intended audience. Like Lotka, much of Odum's influence in ecology, particularly in later years, came indirectly through the writings of others. The reception of *Environment, Power, and Society* was a clear signal that by the early 1970s, he had moved to the fringes of systems ecology and professional ecology in general.

Dealing with Complexity

Arthur Tansley first presented the ecosystem concept within the context of a critique of holism. After more than half a century his trenchant analysis of this philosophical position has lost none of its original bite. Ironically, as it evolved, the ecosystem concept became closely identified with the very philosophy that Tansley so adamantly opposed. This change came about primarily through the writings of Eugene Odum and Howard Odum, strong defenders of holism. Antireductionistic themes increasingly permeated *Fundamentals of Ecology* as it went through three editions. Several other ecosystem ecologists, particularly those drawn to modeling and systems analysis, also claimed to be using holistic approaches in their work. As a result, both adherents and opponents of the specialty have tended to identify ecosystem research with philosophical holism.

Biological debates over holism and reductionism almost always generate more smoke than light, and those in ecology are no exception. As a few perceptive critics have pointed out, Howard Odum's attempt to explain all ecological phenomena in terms of energy looked suspiciously like reductionism, albeit "large-scale reductionism."[58] Conversely, it can be argued that self-styled ecological reductionists have rarely tried to really explain ecosystem phenomena in terms of smaller biological units.[59] They simply ignore the "whole" and study the "parts" in isolation. Such diffuse and polemical debates over reductionism are not uncommon in the history of biology, and more recently some ecologists have been quite sophisticated in explaining the hierarchical relationships among biological systems.[60] But the historical question remains: What purpose did holism play in the early development of the ecosystem concept?

The answer to this question is twofold: holism provided useful rhetorical arguments for justifying and legitimizing an emerging specialty, and it served as a fruitful heuristic for stimulating research. Holistic arguments rarely converted skeptics, but they did increase solidarity within a small group of practitioners. When Eugene Odum arrived at the University of Georgia he encountered a zoology department that was largely indifferent toward ecology. For most of his colleagues, ecology was simply another name for natural history. The idea of ecosystem research was almost totally unknown at the university. Therefore, Odum had to justify not only studying large biological systems but also studying them in terms of their overall metabolism. Moreover, outside this local context where he was attempting to establish an independent institute of ecology, Odum needed to justify the autonomy of ecosystem ecology within the professional discipline of ecology where he was trying to establish a new specialty and within the still broader context of the scientific community where he was competing for funding. In *Fundamentals of Ecology,* Odum presented an unusual and sophisticated defense.

The first part of the argument was antireductionistic. Although nature is organized on many levels, he argued, no level is necessarily more complex or difficult to study than any other.

> *When we consider the unique characteristics which develop at each level,* there is no reason to suppose that any level is any more difficult or any easier to study quantitatively. The enumeration and study of the units of an organism (i.e., the cells and tissues) is not inherently any easier or more difficult than the enumeration and study of the units of a community (i.e., the organisms). Likewise, growth and metabolism may be effectively studied at the cellular level or the ecosystem level by using units of measurement of a different order of magnitude.[61]

To make this point more explicit, Odum drew a diagram of the units of biological organization from cells to the biosphere, but the diagram was arranged horizontally, rather than vertically. The message was clear: if all levels are equally complex, then there is no reason for biologists to adopt a reductionist strategy. Research at the level of ecosystems is just as likely to produce important discoveries as research in molecular biology.

The second part of Odum's argument was more holistic. Dogmatic reductionism impeded the advance of science. If biologists spent all their time studying cells, then they would never get around to studying populations and ecosystems. Furthermore, although all levels of biological organization shared common characteristics (growth, development, metabolism, and homeostasis), the mechanisms by which these processes occurred were different. Understanding a process at one level only partly explained the same process at another level. Knowing about homeostasis at the cellular or organismal levels might provide ecological insights, but it could never completely explain the stability of populations and ecosystems. Thus, science had to advance along a broad front. "This situation is analogous to the advance of an army," Odum concluded, "A breakthrough may occur anywhere, and when one does, the thrust will not penetrate far until the whole front moves up."[62]

Systems thinking often goes hand in hand with philosophical holism. Not surprisingly, the systems ecologists were among its most ardent supporters. Using one of his clever metaphors, Howard Odum referred to the "macroscope" of systems science.[63] In contrast to the microscope that allowed the scientist to observe hidden details, the macroscope served as a kind of "detail eliminator." Through the macroscope large systems appeared simpler; they became black boxes with inputs and outputs. Freed from detail, the systems ecologist could ask new questions about the behavior of the system as a whole. The intricate biological details of a particular ecosystem were relevant; natural history served as an important means of creating an "inventory of parts" for the system, but the real explanation came in terms of overall energy flow through the ecosystem as a whole.[64] For example, when the Odums had studied the metabolism of the reef at Eniwetok Atoll, they were not concerned with individual species. Indeed, at the time they were unable to identify them. Nonetheless, they were able to estimate the total flow of energy through the entire system. Had they started studying the reef from the bottom up, they might never have gotten around to studying its overall metabolism.

A Managerial Ethos

Environmentalists of the 1970s frequently used the ecosystem concept to argue for the preservation of natural habitats. Ecosystem ecologists were also deeply committed to conservation, but not necessarily

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in the form advocated by popular environmental groups. In his bo
Nature's Economy, Donald Worster argues that professional ecologi
are imbued with a "managerial ethos," a set of beliefs that reflect
imperialistic attitude toward nature.[65] Whether or not one complet
accepts Worster's critique, the ecosystem concept did become clos
identified with the rational management of nature for human bene
In the first edition of his textbook, Eugene Odum wrote, "The aim
good conservation is to insure a continuous yield of useful pla
animals, and materials, by establishing a balanced cycle of harvest
renewal. . . . The principle of the ecosystem, therefore, is the b
and most important principle underlying conservation."[66] Ecol
provided an understanding of natural cycles and the homeost
limits of ecosystems. Humans could learn valuable lessons from
ture, but this knowledge also allowed humans to intervene, to man
ulate natural ecosystems, and to create artificial ones.

The idea of "man the manipulator" is a common thread runn
through the literature of ecosystem ecology.[67] For many ecologists
phrase encapsulated the most pressing dilemma facing science
society. Technology, as Odum acknowledged, was a double-ed
sword.[68] It not only held out the promise of a better life, but it
held the potential for destroying the environment. Faced with
dilemma, ecosystem ecologists rarely turned away from technolo
Instead, they often looked forward to a new era of "ecological en
neering."[69] The ecological engineer used nature's own machiner
construct new life support systems for human society. For exam
Howard Odum envisioned a situation where municipal waste wa
might be pumped through a seminatural, aquatic ecosystem. Nu
ents would be removed by microbes that would serve as a base
various food chains. At the top of the food chains might be harv
able species such as crabs. Clean effluent leaving the ecosystem co
be reused as drinking water by the human population. Thus, by c
bining human engineering principles with nature's own "self-des
principles" a true "partnership with nature" might be achieved. M
to the dismay of some traditional environmentalists, such plans w
actually implemented on a small scale, and they apparently wor
quite well.[70]

Peter Taylor has characterized Howard Odum's attitude tow
ecological engineering as "technocratic optimism."[71] However,
technocratic optimism rested uneasily with a more apocalyptic se
that the real cutting edge of technology's sword was its destructi
rather than its productive, edge. Modern industrial society with

voracious appetite for energy and its ability to alter natural ecosystems had precipitated an environmental crisis. In a section of *Environment, Power, and Society*, "The Network Nightmare," Odum used the fantasy of a monstrous computer-organism gone berserk as a metaphor for this crisis.[72] Although he discussed the potential for ecological engineering, Odum suggested that completely managing nature was an impossibility. His brother was also uneasy about the managerial ethos. Homeostasis had evolved gradually in ecosystems, and human perturbations often destroyed the intricate self-regulatory mechanisms of nature. Human domination of nature was a "dangerous philosophy," a belief that Eugene Odum wished to dispel with his *Fundamentals of Ecology*. "When the reader has finished with this book," he wrote, "I am sure he will agree that we cannot safely take over the management of everything!"[73]

Extending the Research Agenda

Raymond Lindeman's trophic-dynamic paper identified three related intellectual problems that together provided the primary foci for ecosystem ecology: biogeochemical cycling, energy flow, and succession. These problems held an intrinsic theoretical interest for those interested in how ecosystems functioned. But for reasons that Lindeman could not have imagined these problems also loomed large in public debates after World War II. Less than a year before Hiroshima, Vladimir Vernadsky wrote that for the first time in history man was becoming "a large-scale geological force."[74] Human activities were now capable of altering not only local environments but also the biosphere as a whole. No example illustrates the convergence of theoretical and practical uses of ecological knowledge so clearly as Howard Odum's dissertation on the biogeochemistry of strontium. When Odum began his research strontium was a substance practically unknown to the nonscientific public. During the late 1940s when Odum began his research, studying strontium was simply another step in G. Evelyn Hutchinson's ambitious biogeochemical survey of the elements. Biogeochemically, strontium acted in a qualitatively similar way to the more abundant and biologically important element calcium. However, the point of Odum's research was to demonstrate that the strontium cycle, or what he referred to as the "strontium ecosystem," was a stable, self-regulating cycle.[75] According to Odum as the concentration of strontium increased in the oceans it was removed and deposited in the exoskeletons of molluscs. As a result of this simple control mechanism strontium was maintained in a steady state equilibrium. He provided data showing that levels of strontium in the oceans had not changed significantly during the past 600 million years.

Odum's early research was the epitome of basic science, and there was no hint that the strontium cycle was of more than purely academic interest. A decade later, atmospheric testing of nuclear weapons and the consequent release of large amounts of radioactive strontium-90 made this element familiar to almost every educated American.[76] By the late 1960s George Woodwell and others demonstrated that toxic substances such as DDT also had biogeochemical cycles.[77] On a local level, these substances could become concentrated in the higher levels of food chains. Global cycles distributed some of these persistent chemicals far from their points of origin. Even Antarctica was not free of pesticide residues. For a public already conditioned by Rachel Carson's *Silent Spring*, such widely publicized revelations heightened environmental concerns. For professional ecosystem ecologists, the discoveries simply confirmed what they already believed: biogeochemical cycles were fundamental processes in all ecosystems.

Biogeochemical cycles were important, but for most ecosystem ecologists energy flow was of even greater interest. As one critic later complained, the specialty seemed to be "obsessed with calories."[78] As the ultimate limiting factor for life, energy flow seemed to hold the key for understanding the structure and function of ecosystems. Expressing the appeal of this line of research, John Teal wrote, "The study of community metabolism is one means of making a functional analysis of an ecosystem. . . . It provides a measure of the total activity of the community just as a study of individual metabolism does for an individual organism."[79] In theory, the structure and function of the living community—the sizes, numbers, and kinds of organisms; the relationship between producers and consumers; competitive interactions among species; the interdependence of predators and prey—could all be explained in terms of energy transformations. As G. Evelyn Hutchinson pointed out in his tribute to the young ecologist, Raymond Lindeman had taken the first tentative steps toward reducing the complexity of ecosystems to such simple energetic terms.[80] Hutchinson's later student, Howard Odum, was primarily responsible for continuing this intellectual process. As Peter Taylor points out, Odum was unique among ecosystem ecologists in that he reduced all ecological parameters—biomass, population sizes, diversity, essential chemical elements—into energy.[81] Following Lotka, he intended to explain ecological phenomena completely in terms of the principles of thermodynamics. Although his grand synthesis, *Environment, Power, and Society*, apparently had little impact on professional ecologists, some of his earlier conceptual innovations were highly influential.

More than any other ecologist, Howard Odum has shaped the way biologists think about energy. The chapters on energetics that he wrote for his brother's textbooks summarized several of his important technical papers and presented this information to a broad audience. Biologists who never read his massive study of Silver Springs, nevertheless absorbed its message through textbook accounts. Perhaps the major conceptual innovation to come out of this study was Odum's pictorial model of energy flow. Unlike earlier diagrams, which confused the movement of energy and material, Odum's model showed at a glance what was important about energy flow. Each trophic level was represented by a rectangular compartment, the size of which represented its energy content. The compartments were connected by arrows representing the flow of energy from one trophic level to the next. Arrows representing the heat loss of respiration were also drawn from each compartment. Diagrammatically the arrows illustrated the effects of the second law of thermodynamics; every trophic transfer entails a loss of usable energy from the system. Like the orbital or "electron cloud" diagrams used by chemists to visualize the probable locations of electrons around the nucleus, Odum's pictorial model played an important explanatory role in ecosystem energetics. Once seen, it became difficult to think about energy flow removed from the visual context of the diagram (figure 8). Not surprisingly, this model appears today in virtually every undergraduate textbook of ecology. Ironically, Odum's later electrical circuit diagrams, which he considered superior to the compartment models, never caught on among ecologists. Pictures are important, and apparently only the right picture can capture the essence of a complex natural process.

Cracks in the Edifice

By the mid-1960s the Odums were at the height of their influence. During this period Eugene Odum wrote perhaps his most important and controversial article, "The Strategy of Ecosystem Development."[82] Published at the end of the decade, the paper was based on Odum's 1966 presidential address to the Ecological Society of America. The apotheosis of the "new ecology," it summarized two decades of research on energy flow and biogeochemistry and placed it within the conceptual framework that the Odum brothers had constructed. Unlike many such articles, however, this was not simply another programmatic statement. In a table, Odum set out a list of twenty-four universal trends that he claimed were characteristic of succession. One might quibble whether these constituted hypotheses and predictions in the technical sense. But the sharp dichotomies that he drew between immature and mature ecosystems were striking, and some ecologists treated them as predictions to be empirically tested.[83]

Strategy meant maximizing stability, a process that occurred on a number of time scales. "In a word," Odum wrote, "the 'strategy' of succession as a short-term process is basically the same as the 'strategy' of long-term evolutionary development of the biosphere—namely, increased control of, or homeostasis with, the physical environment in the sense of achieving maximum protection from its perturbations."[84] If ecosystems actually employed this strategy, a number of measurable changes ought to be observed. During succession diversity should increase as species became specialized for particular functional roles. Therefore, the number of species ought to be greatest in mature, climax ecosystems. Specialization promoted symbiosis as species became more dependent upon one another. In the language of systems ecology, this increase in structural complexity meant an increase in information content and a decrease in entropy in the system as a whole. The growth of decomposer populations and detritus-based food chains would increase the efficiency of nutrient cycling. As a result the leakage of nutrients from the system would decrease. During succession the amount of biomass would increase until it reached a maximum at climax; however, the rate of production in relation to the rate of respiration would decrease. In the climax ecosystem, gross production would roughly equal respiration. In other words, virtually all production would be channeled into self-maintenance, rather than growth. Odum admitted that some of these hypothetical trends were speculative, but he believed that the overall scheme was universally valid. "While one may well question whether all the trends described are characteristic of all types of ecosystems," he concluded, "there can be little doubt that the net result of community actions is symbiosis, nutrient conservation, stability, a decrease in entropy, and an increase in information."[85]

Strategy also had another meaning in Odum's paper. Nature might not have goals, but humans do. Odum complained that the social and economic strategies pursued in industrialized societies were shortsighted and in conflict with natural ecological processes. A decade earlier, he and his brother had contrasted the natural stability of the coral reef at Eniwetok with the chaos produced by World War II.[86] By the end of the 1960s natural models for human society seemed even more appropriate. The successional trends that he had identified with stable, mature ecosystems also served as guides for rational agricultural and industrial development. The strategy of ecosystem development was also a prudent strategy for human social development.

Comparing nature's strategies with human strategies was a clever literary device. Even without its set of concrete predictions about the effects of succession, Odum's paper would have been memorable as a statement of environmental principles. But by the end of the 1960s many ecologists were becoming impatient with talk of evolutionary or ecological strategies. It sounded perversely teleological, and it could be seriously misleading. The initial volleys of this dispute had actually occurred several years earlier at the 1959 meeting of the Ecological Society of America. During a symposium on energy flow, Howard Odum introduced his electrical circuit diagrams of ecosystems. In the ecological case, Odum claimed that energy was driven by an "eco-force" analogous to voltage in the electrical circuit. This, according to Odum, necessitated a fundamental change in the way ecologists thought about predator-prey relationships. "The validity of this application [Ohm's Law] may be recognized," he asserted, "when one breaks away from the habit of thinking that a fish or a bear catches food and thinks instead that accumulated food by its concentration practically forces food through the consumers."[87] This rather non-biological interpretation of predation apparently struck many in the audience as ludicrous. Odum, himself, later admitted that it had alienated him from many ecologists.[88]

This early episode highlighted a serious intellectual problem in ecosystem ecology. Treating trophic levels as black boxes with energy inputs and outputs had proved to be a powerful investigative tool, but when pushed too far it could also mislead. Thermodynamically, there might be nothing wrong with the idea of prey being forced down the throats of predators, but biologically there certainly was. The living world simply did not operate that way. Although less extreme, Eugene Odum's "Strategy of Ecosystem Development" suffered from the same defect. The idea of strategy was obviously a metaphor, but it seemed to suggest that ecosystems had goals and that the parts of the system played functional roles toward achieving those goals. Not only did this imply teleology, but it also ignored fundamental evolutionary principles.[89] By the end of the 1960s most evolutionary biologists believed that natural selection operated upon individuals, not upon collections of individuals. Even metaphorically, ecosystems could not have strategies.

The "Strategy of Ecosystem Development" was frequently cited, but it was also widely criticized.[90] It appeared during an important time of transition in ecology. By the end of the 1960s ecosystem ecology was a well-established specialty, but it was facing increasing opposition from other groups of biologists. Contrary to Eugene Odum's hope that all ecologists would rally around the ecosystem, the discipline was becoming increasingly divided. The sources of this conflict are explored more fully in the next two chapters.